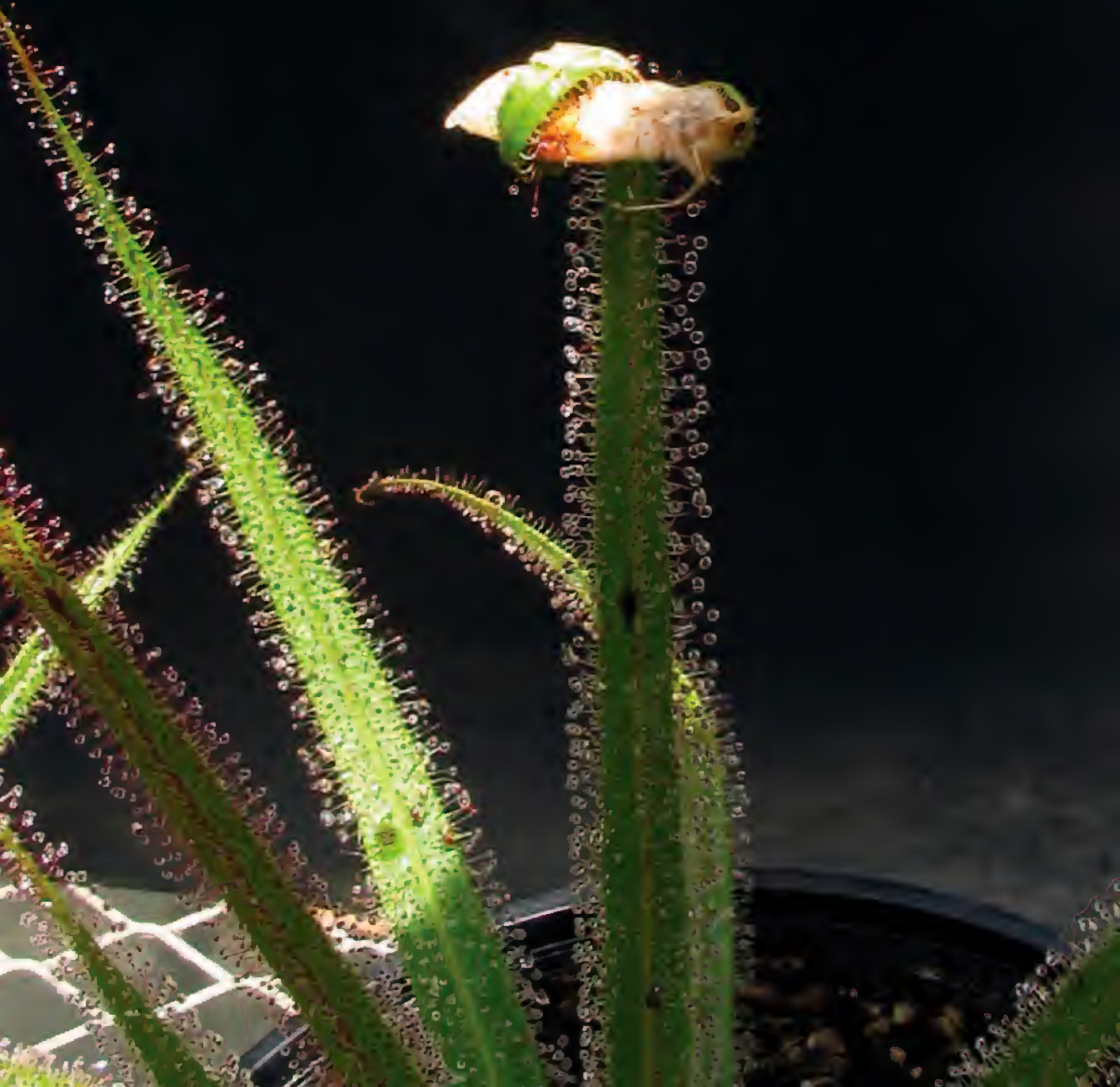


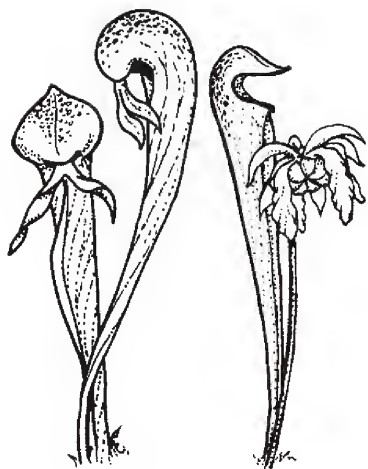
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Front Cover: A hapless moth ensnared by a vicious *Drosera regia*. Photo by Bob Ziemer. Article on page 109.

Back Cover: Damon Collingsworth communing with *Sarracenia leucophylla* at Splinter Hill Bog Preserve near Rabun, Alabama late in the day. Photo by Damon Collingsworth. Article on page 113.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

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CONTENTS

News in ecophysiological research on aquatic <i>Utricularia</i> traps -----	92
Nutrient stoichiometry of <i>Nepenthes</i> species from a Bornean peat swamp forest -----	105
<i>Drosera regia</i> Stephens -----	109
A surprise in the gloaming: A field observation at Splinter Hill Bog Preserve, Alabama -----	113
<i>Drosera burmannii</i> : A carnivorous plant species from eastern Ghats of India -----	115
New cultivars -----	116
Literature reviews -----	121
Book review -----	122

FROM THE PRESIDENT

Our Mission: *To provide for informational and educational exchanges on all aspects of carnivorous plants, to support horticultural and scientific studies of carnivorous plants, to encourage the cultivation, conservation, and appreciation of carnivorous plants, and to aid in the propagation and dissemination of carnivorous plants.*

Over the past six months to a year I've been struck by how fully ICPS members and people from the general CP community embrace or participate in the ICPS mission. It is an exciting time – all over the globe people are writing individual blogs, participating in on-line discussion forums, organizing local carnivorous plant clubs and societies, providing educational and conservation talks and hosting plant shows.

One of the big things that happened recently was the ICPS2012. The time, effort, and dedication of members coordinating and attending events like ICPS2012 help further the mission of the ICPS – thank you to the New England Carnivorous Plant Society for hosting! It's always exciting to hear how far people travel from around the world to attend.

Something great about the CP community is not only its passion and international diversity, but the diversity of age across the community. From youth to elders, we have a wide age range of those passionate about CPs. In order to further our efforts to cultivate informational and educational exchanges on all aspects of carnivorous plants across our diverse community we use a range of print, electronic, and social media tools.

As the range and use of communication and social media tools continues to grow – we are also continuing to evolve and are interested in using all the tools we can to continue our mission, and in the process nourish and cultivate a vibrant CP community.

So, how can you help? Here are a couple easy things you can do:

- Volunteer – if you have an idea that will assist in the ICPS mission and the dedication to carry it out, let us know.
- Submit an article to the CPN – we're always on the lookout for articles, essays, and reports from the CP community. While we do have some more scholarly science based articles, ICPS members are always excited and interested in hearing about your cultivation tips and tricks, and field reports!
- While keeping the ICPS mission in mind, I encourage you to explore the ICPS social media outlets – the Forum, Facebook, ICPSTv on YouTube, and Flickr. After you check them out I'd like to hear from you, general users to the social media super users. Are we using these to the fullest potential? Are there other social media outlets or uses we should think about using? Please send me your thoughts on how we can use social media to its' fullest potential to further the ICPS mission.

I look forward to hearing from you!

MIKE BALDWIN

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NEWS IN ECOPHYSIOLOGICAL RESEARCH ON AQUATIC *UTRICULARIA* TRAPS

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Keywords: ecophysiology: aquatic *Utricularia*, traps.

This paper is dedicated to the memory of Dr. Peter Taylor who contributed invaluable to the knowledge of the genus *Utricularia*.

Introduction

Aquatic carnivorous plants comprise the species *Aldrovanda vesiculosa* L. (Droseraceae) and about 50 species of the genus *Utricularia* L. (Lentibulariaceae; Taylor 1989). Aquatic *Utricularia* species usually grow in shallow, standing humic waters which are usually poor in N and P, but occasionally also in K (Adamec 1997; Guisande *et al.* 2007). Although they take up all necessary nutrients either directly from the water by their rootless shoots or from animal prey by traps, under favorable conditions, they exhibit very rapid apical shoot growth of 3-4 leaf nodes d⁻¹, while their shoot bases decay at this same high rate (Friday 1989; Adamec 2009).

The *Utricularia* traps have always fascinated scientists: they are the smallest among those of carnivorous plants but are arguably the most sophisticated and intricate. One composed leaf of aquatic *Utricularia* usually bears dozens to hundreds of oval-shaped, fluid-filled traps of foliar origin (see Figs. 1, 2). As opposed to their terrestrial counterparts having only tiny traps (0.5-1.5 mm), aquatic or amphibious *Utricularia* species have much larger traps which have exclusively been used for physiological research (Taylor 1989; Adamec 2011a). These bladders are typically 1-6 mm long with elastic walls two cell layers thick and have a mobile trap door (see *e.g.*, Juniper *et al.* 1989 or Adamec *et al.* 2011 for detailed structure). The inner part of the trap is densely lined by large glands of two types: quadrifid glands cover almost the whole inner surface and take part in the secretion of digestive enzymes and in the resorption of released nutrients, while the smaller bifid glands,



Figure 1: Traps of *U. arnhemica* ca. 2 mm large from a tissue culture. All photos L. Adamec.



Figure 2: Traps of *U. foliosa* are very slimy.

which are located near the door, take part in pumping out the water. The traps capture small aquatic animals, usually 0.5-2 mm long, and these are mostly zooplankton. These basic characteristics of *Utricularia* trap functioning based on several “classic” studies have been known and compiled in a stagnant form for decades. Nevertheless, within the last five years (2007-2011) with the boom in 2011, many novel physiological, biophysical, and ecological works have been published and crucially extended our knowledge of the trap functioning, often changing our basic understanding of these processes. These recent studies based on very advanced methods partly answer the following questions: How do these perfect traps function, then kill and digest their prey? How do they provide ATP energy for these demanding physiological functions? What are the nature of the interactions between traps and the mutualistic microorganisms living inside them as commensals? In this mini-review, all of these questions are addressed from an ecophysiological’s point of view, based on the most recent literature, data, and unpublished results. Inspirations for further research on this fascinating topic are also suggested.

Trap Functioning in “Classic” Studies

Almost all of the knowledge of the biophysical nature of *Utricularia* trap functioning was published in a series of only four famous studies conducted between 1973-1985 (Sydenham & Findlay 1973, 1975; Sasago & Sibaoka 1985a,b). These studies are based on tricky measurements of negative pressures inside the trap and water outflow by piercing the isolated trap with fine glass capillaries (outer tip diameter 20-50 μm). The trap thickness was simultaneously optically or mechanically monitored as a reliable measure of trap water flow and the negative pressure. It is very curious that nobody (except for Singh *et al.* 2011) has successfully repeated this simple capillary method due to water leakage.

The trap is hermetically sealed and a negative pressure of about -16 kPa (*i.e.* 1/7 bar) relative to the ambient water is maintained inside a fully reset trap. When a prey species touches sensory hairs situated on the trap door it opens, the small animal is aspirated into the trap and the door closes again. This process of firing is complete within 10-15 ms and is the most rapid plant movement known (Sydenham & Findlay 1973). Immediately after firing, the negative pressure inside the trap drops to zero, but is soon restored by the rapid removal of *ca.* 40% of the water from the fired trap until the original concave shape is reached. This aspect of trap resetting lasts about 25-30 min and the trap is ready to fire again; the full resetting process lasts much longer. Using very inventive methods, the authors (Sydenham & Findlay 1973, 1975; Sasago & Sibaoka 1985a,b) have also found that water is pumped out of the traps by an active process associated with a consumption of the metabolic energy of ATP. When inhibitors of aerobic respiration were added to the trap fluid, the water pumping and trap narrowing processes were very markedly blocked.

How is water pumped out of the traps? The authors have found that bifid glands attached close to the trap door take part in water pumping and that water is exuded from the pavement epithelium close to the door. Electrophysiological measurements have led to the hypothesis (Sydenham & Findlay 1975; Sasago & Sibaoka 1985a) that Cl^- ions are actively taken up from the trap fluid by the bifid glands and, due to their movement, osmotically drag water molecules. Monovalent cations (Na^+ , K^+) accompany the Cl^- fluxes, while divalent cations (Ca^{2+} , Mg^{2+}) rather inhibit them. The second part of the water pathway is still, however, veiled in mystery as it appears that the water is expelled from the cells of the pavement epithelium by the turgor pressure through a very leaky plasmalemma (for solutes <600 Daltons; Sydenham & Findlay 1975). Traps can also pump out water in moist air or when immersed in a liquid paraffin oil (Sasago & Sibaoka 1985a).

Food Web Inside the Traps

Traps of aquatic *Utricularia* possess one significant ecological trait which is their principal difference from snapping *Aldrovanda* traps. This could offer unexpected ecological possibilities for the plants. In spite of its tiny volume, the trap fluid in *Utricularia* plants is inhabited permanently by various commensal microorganisms – bacteria, cyanobacteria, microfungi, algae, euglenes, dinophytes, protozoa (ciliates), and rotifers – which live in a mutualistic interaction with the plant (*e.g.*, Richards 2001; Peroutka *et al.* 2008; Alkhalaf *et al.* 2009; Sirová *et al.* 2009; Płachno *et al.* 2012). These organisms enter the traps from the ambient environment, propagate inside the traps and take part in prey decomposition. Recently, evidence for the formation of a miniature food web has been provided in two Central American *Utricularia* species (Sirová *et al.* 2009). Similar food webs have also been described in digestive fluids of large pitcher-shaped traps of several species and genera of terrestrial carnivorous plants (*Darlingtonia californica*, *Sarracenia purpurea*, *Nepenthes* spp.; Juniper *et al.* 1989). In *Utricularia* traps, due to methodical limitation, it may not be clear which microorganisms found inside the traps are living as commensals and which are prey (Peroutka *et al.* 2008; Alkhalaf *et al.* 2009, 2011; Płachno *et al.* 2012).

Oxygen Regime Inside The Traps and Trap Respiration

Oxygen concentration in the *Utricularia* trap fluid may be considered the crucial characteristic, not only for trap respiration and water pumping but also for life and propagation of the commensal communities and the death of the prey. Using a miniature oxygen sensor, almost zero $[O_2]$ were measured in the trap fluid of mature empty traps of 6 aquatic *Utricularia* species with larger traps (Adamec 2007). The median steady-state $[O_2]$ values were within 0.0–4.7 μM , but usually only within 0.0–1.4 μM (*i.e.*, 0.00–0.04 $mg \cdot l^{-1}$ or 0.0–0.5% of O_2 saturation), both in isolated traps and those on intact shoots bathed in stirred, aerated media. These results are independent of irradiance and O_2 oversaturation in shoot tissues. Thus, even in spite of some leakage of oxygenated water into the measured traps and O_2 diffusion from the trap wall intercellulars, the internal trap structures are able to consume the O_2 rapidly to cause anoxia. After the minisensor tip had been inserted into the trap lumen, the trap fluid $[O_2]$ declined linearly almost to zero within 10–100 min. The linear rate of the decline is a measure of the respiration rates of internal trap structures and commensal organisms offset by O_2 influx from the trap walls. It may be inferred that under natural growth conditions, long periods (hours to 20 h) of anoxia inside the traps are interrupted by short periods (20–100 min) of higher $[O_2]$ after stimulated or spontaneous firings. Therefore, captured organisms either die of O_2 deprivation and are prey, or are able to tolerate anoxia and are commensals. *Utricularia* traps likely kill their prey by suffocation. Prey digestion inside the traps did not increase the “external” dark respiration rate (R_p) of traps (Adamec 2006). Though photosynthesis in *Utricularia* shoots (*i.e.*, O_2 oversaturation in the shoot tissues) leads to a much greater O_2 influx to the trap lumen than from a stirred, aerated ambient medium in darkness, the steady-state $[O_2]$ in the trap fluid is zero in both cases (Adamec 2007). In conclusion, the anoxic trap fluid of intact traps is well isolated from the oxygenated ambient water from the trap walls such that O_2 from the ambient water is not transferred inside the traps. As opposed to these isolated traps, open pitchers of *Sarracenia purpurea* exhibit only a reduced $[O_2]$ in their viscous fluid (Wakefield *et al.* 2005) but their prey dies in the same way of suffocation.

The discovery of internal trap anoxia raises some important ecophysiological questions. Due to

their very demanding functions, *Utricularia* traps are metabolically very active and their R_D per unit fresh or dry weight is 2-3 times greater than that of leaves or shoots bearing these traps (Adamec 2006). Moreover, as found in the four classic studies, pumping the water out of the traps strictly requires the participation of aerobic respiration inside the traps. It can be assumed that it is the high R_D of internal bifid and quadrifid glands and pavement epithelium that are responsible for the high trap R_D due to the presence of abundant mitochondria and transfer cells in all these structures (Sasago & Sibaoka 1985a; Płachno & Jankun 2004). From a biochemical point of view, however, it is unclear how the internal trap glands provide ATP energy to maintain their demanding physiological functions (water pumping) under (almost) anoxic conditions for many hours or even permanently (Adamec 2011b,c; Vincent *et al.* 2011). Based on molecular findings, a link between faster reaction kinetics of *Utricularia* traps and a mutation occurring in the mitochondrial respiratory chain enzyme cytochrome *c* oxidase has been suggested (Jobson *et al.* 2004). Within Lentibulariaceae, this mutation has only been detected in *Utricularia*, but not in the sister genera *Pinguicula* and *Genlisea* with immobile traps. The authors (Laakkonen *et al.* 2006) further hypothesize the decoupling of mitochondrial proton pumping from electron transfer, which could be a rich source of ATP energy after trap firing during the aerobic period. Such decoupling would allow the traps to optimize power output during times of need, although with a 20% decrease in total energy efficiency of the respiratory chain. For some important reasons, it seems improbable that the traps provide most of their ATP energy need from anaerobic fermentation. On the contrary, it is highly probable that the inner trap structures possess an extremely high O_2 affinity (well below 0.5-1 μM , which is beyond the resolution of the Clark-type O_2 sensor), using the permanent O_2 influx from the trap wall intercellulars. This suggestion has recently been supported by the finding of very high O_2 affinity of respiratory enzymes in terrestrial plant leaves (0.3-1.1 μM ; Laisk *et al.* 2007). The above mentioned mutation in the cytochrome *c* oxidase could account for such a high O_2 affinity. Finally, transcriptomic global gene expression analysis in *U. gibba* has recently confirmed that traps significantly over-express genes involved in respiration (Ibarra-Laclette *et al.* 2011).

It seems the extremely low $[O_2]$ in the trap fluid is thus a result of a functional compromise: it must be very low to reliably kill the captured prey (requiring *ca.* >15-30 μM) but higher than a threshold for an effective aerobic R_D (>*ca.* 0.4 μM). Following from direct gasometric measurements, even abundant microbial commensal communities in old *Utricularia* traps do not affect crucially the O_2 regime inside the traps: their R_D was between *ca.* 5-50% of the total “internal” trap R_D and their net photosynthetic rate in light did not extend the R_D of the inner trap structures, either (Adamec, unpubl.).

Regulation of the Investment in Carnivory

In wide-spread *U. australis*, traps usually represent only about one-third of dry biomass of mature shoot segments as a structural investment in carnivory (*i.e.*, structural cost; Adamec 2008) but the total trap R_D amounted to 67% of the total shoot R_D (Adamec 2006). If the net photosynthetic rate of traps of aquatic *Utricularia* (per unit fresh weight) reached only 7-10% of the values for leaves or shoots even under optimum conditions (Adamec 2006), then this combination means that traps represent a very high energetic (metabolic) cost for the plants. Moreover, as found recently (Adamec 2008, 2010), the traps also represent a high mineral cost, especially for N, P, and K, and can contain 12-69% of the total plant amount of these nutrients. Therefore, the proportion of trap biomass to the total plant biomass is under a purposeful ecological regulation. The regulation includes two steps: the supreme step is high $[CO_2]$ as a prerequisite for high photosynthetic rate (posi-

tive feed-back), while the second step is tissue N or P content in young shoot segments as a negative feed-back. When [CO₂] is short (*e.g.*, in oligotrophic sand-pits) the mineral regulation is inefficient (Adamec 2008, 2009). However, in different species, the regulation depends on different nutrients: in *U. australis*, it is only N (Adamec 2008; Sirová *et al.* 2011), but only P in *U. vulgaris* (Kibriya & Jones 2007), while both N and P in *U. foliosa* (Bern 1997).

Production of Digestive Enzymes

Little is still known about prey digestion in *Utricularia* traps though standard biochemical techniques revealed the presence of proteases in the trap fluid as early as the 1920s (Juniper *et al.* 1989). Later, protease, (acid) phosphatase, and esterase were localised cytochemically in the digestive quadrifid glands (Heslop-Harrison 1975; Vintégoux & Shoar-Ghafari 2005) with phosphatase also on their surfaces (Sirová *et al.* 2003; Plachno *et al.* 2006). Activities of 5 hydrolases (phosphatase, aminopeptidase, β -hexosaminidase /chitinase/, α - and β -glukosidase) were measured microfluorimetrically directly in the filtered trap fluid collected from both empty traps of four aquatic *Utricularia* species and their culture water (Sirová *et al.* 2003). Phosphatase invariably exhibited the highest activity, while the activities of the other enzymes were usually lower by one or two orders of magnitude. As the activities of the other enzymes in the trap fluid were usually lower than in the ambient culture water, the enzymes could have entered the trap from the ambient water. However, the trap fluid phosphatase exhibited its highest activity at a pH between 4.7-5.5, while that in the ambient water occurred at a higher pH of 9.0. It has been confirmed recently for some *Utricularia* species that traps produce the phosphatase continuously and independently of prey capture (Sirová *et al.* 2003), loading with N or P salts, or enrichment of the culture water in mineral N and P (Adamec *et al.* 2010). As follows from both latter papers, trap age is the key factor in the patterns of phosphatase production. It is possible that old, still functional traps shift their function from enzyme production towards nutrient uptake (Sirová *et al.* 2009). Trap fluid pH in most of the examined species was usually within a narrow range from 4.8 to 5.1 and seemed to be regulated by the traps (Sirová *et al.* 2003, 2009; Adamec *et al.* 2010).

One surprising aspect of these enzyme studies should be pointed out. In all species studied (excepting *U. foliosa*) and under all experimental conditions, very low or even zero activity of aminopeptidase (*i.e.*, protease) was found in the fluid in traps with or without prey (Sirová *et al.* 2003, 2009; Adamec *et al.* 2010). However, on the basis of a very efficient total N uptake from prey in *U. vulgaris* traps (Friday & Quarmby 1994), it is evident that proteinaceous N as the main N source from prey must also be effectively digested and absorbed. Moreover, the aminopeptidase found inside the traps had its optimum pH between 7.0 to 9.0, but zero activity at pH 4.7 and much resembled that found in the ambient water; the activities in both environments were also very similar. Thus, a great deal of the very low aminopeptidase activity enters the traps from the ambient water. The absence of aminopeptidases in the fluid could be compensated for by the autolysis of dead prey tissues. Yet the discrepancy between the findings of very low or zero protease activity in the trap fluid with or without prey, and in the presence of large secretory vesicles (Golgi apparatus) rich in proteases in quadrifid glands (Heslop-Harrison 1975; Vintégoux & Shoar-Ghafari 2005) still cannot be explained. As proteases commonly have a very diverse substrate specificity, it is possible to suspect the used microfluorimetric method involves only a minor part of all present proteases in the fluid.

Similarly, the same discrepancy exists between the invariably high phosphatase activity found in the trap fluid and a very low activity of enzyme labeled fluorescence (ELF) of phosphatase usually detected on the surface of quadrifid glands (Sirová *et al.* 2003; Adamec *et al.* 2011). At least a part of this

discrepancy might be explained by methodical limitation of the ELF method (*cf.* Płachno *et al.* 2006). Moreover, it is not clear which proportion of any enzyme activity in the filtered trap fluid is produced by trap glands alone or various trap commensals, in addition to an unknown part of the activity gained from the ambient water. Evidence has recently been provided using the ELF method that some commensals in the trap fluid (algae, bacteria) exhibit a considerable phosphatase activity on their surface (Płachno *et al.* 2006; Sirová *et al.* 2009). Consistently high trap fluid activities of phosphatases in all species imply that P uptake from prey or detritus might be more important than that of N for the plant.

The Importance of Commensals in *Utricularia* Traps

As mentioned above, an abundant community of commensal microorganisms occurs inside aquatic *Utricularia* traps and is denser in older traps. Due to green euglens or other algae, they are greenish. Though the first data on species composition of the community are over 130 years old their importance for *Utricularia* ecophysiology is still quite unclear. One must emphasise that, in spite of their undeniable perfect functional features, aquatic *Utricularia* traps capture relatively little animal prey in barren, nutrient-poor waters though a high abundance of commensal organisms also occur in empty traps (Richards 2001; Peroutka *et al.* 2008; Adamec 2008, 2009; Sirová *et al.* 2009; Płachno *et al.* 2012). Starting with the novel study by Richards (2001) it has therefore been assumed in these studies that a mutualistic interaction between the plant and trap commensal community prevails over catching animal prey for mineral nutrient uptake in these barren waters.

Trap commensal microorganisms are not strictly specialised to living inside the traps. They can live either as periphyton on the external plant surface or freely as plankton in the ambient water and may be considered generalists (Peroutka *et al.* 2008; Alkhalaf *et al.* 2009, 2011; Sirová *et al.* 2009). All of these studies have also suggested a considerable potential importance of phytoplankton for mineral nutrition of (European) aquatic *Utricularia* species. A high proportion of traps contained the same planktonic algae as in the ambient water but about 90% of them were dead and thus served as prey (Peroutka *et al.* 2008). They entered the traps due to an incidental firing. That is why the authors have named their paper appropriately: “*Utricularia* – a vegetarian carnivorous plant?” In the study from northeastern Germany, 60% of all animals found inside traps were ciliates (Alkhalaf *et al.* 2009; *cf.* Płachno *et al.* 2012). In species with dimorphic shoots (*U. intermedia*, *U. floridana*), the carnivorous shoots of which grow down to a loose peaty substrate, an incidental aspiration of brown detritus (rich in humic acids) could also be of a similar nutritional importance (see Fig. 3).

A great accumulation of nutrients inside the traps without prey has been proven. In *U. foliosa* and *U. purpurea* growing at an oligotrophic site in Belize, surprisingly high concentrations of both organic and mineral dissolved substances were found in the filtered trap fluid in all trap age categories (in mg.l⁻¹): C, 64-307; N, 7-25; P, 0.2-0.6 (Sirová *et al.* 2009). Nevertheless, the total content of both C, N, and P in the trap fluid, including mainly the particulate form (*i.e.*, the commensal organisms and detritus), was several times greater (in mg.l⁻¹): C, 632-1570; N, 21-81; P, 0.9-4.2. The total nutrient content usually correlated with the increasing trap age. On the basis of phospholipid fatty acid analysis of the trap commensal biomass, the occurrence of a complex microbial food web in the trap fluid was revealed, with bacteria forming >75% of the viable microbial biomass. The authors thus assumed that trap commensals could play a role in N and P uptake by the traps in barren waters without prey.

In a two-day experiment on *U. australis* and *U. vulgaris* using ¹³C, a great proportion of newly fixed CO₂ was allocated from shoot bases not only to shoot apices, but also to mature shoot segments (Sirová *et al.* 2010). Total carbon allocation in plant tissues rapidly decreased with increasing age of the shoot segments but the ratio of C exuded into the trap fluid to that in plant tissues

increased markedly with age – twice as much newly fixed C was allocated into the trap fluid than the plant tissue in the oldest analyzed segments. Overall, 20-25% of the newly fixed C was allocated into the trap fluid. Sirová *et al.* (2011) have recently proven that C exudates fuel respiration of the prevailingly heterotrophic microbial commensal community within the empty traps of three aquatic *Utricularia* species. Up to 30% of the total dissolved organic C analyzed in the trap fluid were easily metabolized compounds (mainly glucose, fructose, sucrose, and lactate) and the proportion of exuded compounds, as well as their microbial utilization, decreased with increasing mineral nutrient supply (N, P) and trap age. The total concentration of 46 analyzed organic compounds in the trap fluid ranged between *ca.* 30-150 mg.l⁻¹ (*i.e.*, 1.2-8.7 mM of organic C); comparable values between 9-78 mg.l⁻¹ were found in another study in three *Utricularia* species (Borovec *et al.*, unpubl.). Moreover, shaded plants exhibited lower concentrations of organics in their trap fluid. This extensive C supply to the trap fluid is undoubtedly an important additional maintenance (energetic) cost of traps. It is thus possible to conclude that the dominant part of C in the commensal organisms is provided by the plant (Sirová *et al.* 2009, 2010, 2011). Yet, on the basis of record high photosynthetic rate of photosynthetic *Utricularia* shoots (Adamec 2006) the plants can afford such “garden-ing” despite their very rapid growth. Beneficially, the plant could gain growth-limiting N and P from phytoplankton and detritus decomposed in the fluid of traps without any animal prey. Nevertheless, this N and P input from the ambient medium to the traps has never been experimentally quantified (but see below). It can be concluded that the concentration of organic compounds in the trap fluid is partly species specific and depends on cultivation conditions (irradiance) and water chemistry. High concentration of organic acids in the fluid could determine the low pH values of about 5 (Sirová *et al.* 2003, 2009; Adamec *et al.* 2010) indicating also a high buffering capacity.

Rapid Trap Movement, Spontaneous Firings, and Permanent Water Flow

In 2011, several papers were published which crucially changed and specified our understanding of the biophysical processes associated with *Utricularia* trap firing. The unique use of a high-speed camera has revealed that the essence of the reversible trap door opening and closing is the rapid curvature inversion called buckling and unbuckling (Joyeux *et al.* 2011; Singh *et al.* 2011, Vincent *et al.* 2011a,b; Vincent & Marmottant 2011). As a result of the negative pressure inside the trap, the curved trap door is metastable and any tiny mechanical perturbation (mediated by prey through the trigger hairs) triggers the curvature inversion (buckling) leading to trap opening and inflation. When the negative pressure is gone, the trap door spontaneously returns to its initial curvature, closing the door again. Thus, the negative pressure inside the traps is an essential component part of the opening and closing mechanism. Moreover, the complete process of trap firing was specified to last only 2-5 ms in several species.

New important challenges for *Utricularia* trap ecophysiology have very recently arisen from the discovery of spontaneous firing in *Utricularia* traps. Using both a high-speed camera for intact shoots (Vincent *et al.* 2011a,b) and a linear position sensor for excised traps (Adamec 2011b,c), a more or less regular trap firing without any mechanical stimulation was confirmed in several aquatic *Utricularia* species and in two trap age categories. Spontaneous firings occurred 0.3-2.4 times during the 1-day resting period and the mean time between two spontaneous firings varied between 5-16 h. Quantitatively (trap thickness increase due to firing, resetting rate), spontaneous firings resembled mechanically stimulated ones (Adamec 2011b). In two *Utricularia* species, Vincent *et al.* (2011b) subdivided the traps after the time patterns of spontaneous firings into metronomic, random and bursting. It is possible that a spontaneous firing occurs as a “safety valve” protecting the integrity of the trap door. It was also found that the traps pumped water out after firing for at least 5-10 h until a steady-state was attained (Adamec 2011b).



Figure 3: Traps of *U. intermedia* are born only on carnivorous shoots. Some traps are full of dark peaty detritus.

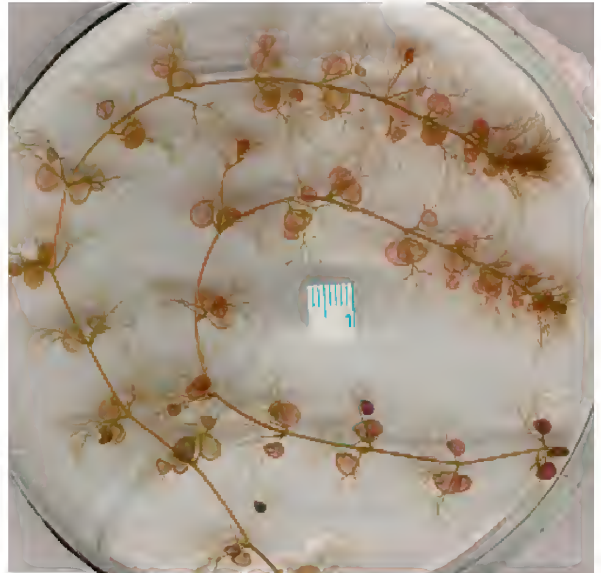


Figure 4: Traps of African *U. reflexa* (from Botswana) can be to 6.5 mm large in an indoor culture and are conveniently used for experiments.

As opposed to Sydenham & Findlay (1973) who postulated a concept of an internal negative pressure sensor regulating water pumping in the trap, the most recent data (Adamec 2011c) suggest a permanent pumping out of water from the traps. These data are based mainly on the fact that no lag-period in water pumping from the trap was detected within the first 2 s after trap firing, which occurred after a 3-h resetting period. This can mean that either the water permanently recirculates through some leaks under the trap door or the mechanism of water pumping becomes thermodynamically inefficient at high negative pressure though it runs permanently.

Taxonomic aspects and basic functional characteristics of trap firing (magnitude of firing and resetting rate as “trap efficiency”) were compared in 13 aquatic *Utricularia* species of the mean trap length between 2.0 to 5.3 mm (Adamec 2011c). On the absolute scale, the 13 species differed considerably in their firing and resetting rates. Significant interspecific differences were also found in the magnitude of firing (in total 3.7-4.2 times) and resetting rates (10-24 times) per unit trap thickness or length. Overall, traps of *U. australis*, *U. stellaris*, and *U. inflata* showed the greatest firing and resetting rates. The relative magnitude of firing per unit trap thickness or length showed a highly significant negative correlation with both trap thickness and length and the same also held for the relative resetting rates. Smaller and narrower traps are thus relatively more effective at trap firing and resetting than larger traps. Neither firing nor resetting characteristics were significantly different between unfed and prey-fed traps of *U. reflexa* (see Fig. 4) and this was also true for the occurrence of spontaneous firings.

Ecological Consequences of Water Flow

Obviously, the most recent findings on trap operation – spontaneous firing and water recirculation – can better explain how growth-limiting N and P enter the traps from the ambient medium and become a substrate for the microbial food web. It is therefore evident that spontaneous firing of each trap, which occurs on average several times a day, could lead to a substantial gain of N and P for the

traps. During its three-week life-span, each trap can aspirate around 15 times its own volume in surrounding water (40% trap volume \times 2-daily spontaneous firings \times 20-day life-span). If the trap commensals help to decompose this “non-animal” prey, it could theoretically imply a significant N and P gain for the plant, especially for those plants in barren waters which trap few animals. The literature assumed that this N and P gain by empty traps could be ecologically important but no quantification has been given so far (Richards 2001; Peroutka *et al.* 2008; Alkhalaf *et al.* 2009, 2011; Sirová *et al.* 2009, 2010; Adamec 2011b). When, however, one considers the published data on the mean total N and P content (both dissolved and particulate, see above) within a middle-aged trap of *U. purpurea* and *U. foliosa* (Sirová *et al.* 2009) and the mean total N and P content at natural oligo- and mesotrophic sites of *U. australis* in the Czech Republic (Adamec 2008), a simple budget model of N and P gain can be made. When water recirculation through the traps is accounted for then, surprisingly, only a very slow accumulation of total N and P within empty traps can occur (see Adamec 2011c for all details). [Model data: trap volume 5 μl , water recirculation rate 1 $\mu\text{l}\cdot\text{h}^{-1}$ for 20 h a day, only $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ influx from the ambient water, mean natural concentrations of $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ at the sites; Sasago & Sibaoka 1985a,b; Adamec 2008, 2011c]. Simply, it would take between 40-70 days for an empty trap to accumulate the measured N or between 15-23 days for them to accumulate the P if there were only spontaneous firing and water recirculation mechanisms occurring. By the application of the model data for the relationship between trap volume and biomass and for shoot N and P content in *U. australis*, one can further estimate that the total N and P amount inside the traps represents only about 3.5% of total plant N and 1.2% of P (Adamec 2011c).

Several Conclusions Can Be Drawn From These Model Data.

1. The calculated N and P input rates from the ambient water due to both spontaneous firings and hypothetical water recirculation are so low that each trap without prey can only reach these nutrient levels after a long time, which is comparable with or even longer than the trap life-span. Thus, such a low N and P gain cannot be ecologically important for the plant mineral nutrition at all but the rapid turnover of N and P inside the traps can be.
2. Since even young *Utricularia* traps (*ca.* 1 week old) contained a relatively high total N and P content comparable with that in the older traps (Sirová *et al.* 2009), the traps could take up neither N nor P from the trap fluid for the plant itself as the total N and P content in the trap fluid would have been much lower.
3. To account for all of these findings, it is evident that the traps exude not only organic C into the fluid (Sirová *et al.* 2010), but also N and P to enhance the microbial community. This idea can be supported by the finding of a growth reduction of terrestrial *U. uliginosa* after addition of euglens to peaty soil (Jobson *et al.* 2000). It is possible that inoculation of young traps by microorganisms stimulates the traps to exude both organic C and also N and P. Therefore, it seems that *Utricularia* traps without animal prey have no nutritional benefit from the trap commensal community and that the trap microorganisms behave rather as parasites than commensals. The extent of this N and P exudation to the trap fluid can only be a few % of the total plant N and P amount.
4. *Utricularia* species commonly grow in very oligotrophic, barren waters with very low prey availability (Friday 1989; Adamec 1997, 2008, 2009; Richards 2001; Guisande *et al.* 2007; Peroutka *et al.* 2008; Sirová *et al.* 2009). It can be inferred that the N and P uptake affinity of *Utricularia* shoots is very high (the limits for uptake should be below 1 μM for NH_4^+ and 0.1 μM for phosphate), while that for N- and P-containing substances in the traps without prey can be very low or zero (*cf.* Sirová *et al.* 2009).

5. If the trap microorganisms are beneficial for the plant, the ecological benefit can occur only in traps with captured prey to facilitate prey digestion. The trap microorganisms in traps represent additional ecological costs for trap maintenance. It may be hypothesized that plants keep up their trap commensal community (“gardening”) by exudation of organic and mineral nutrients into all traps, as an offset for better prey digestion only in the traps with captured animal prey and, thus, for greater uptake of mineral nutrients from prey. This should lead to a final ecological nutritional benefit for the plant. The real cost:benefit ratio depends on the proportion of traps which capture animal prey during their life.
6. Aquatic *Utricularia* species invest more in trap production at low tissue N and/or P content in shoots (Bern 1997; Kibriya & Jones 2007; Adamec 2008; Sirová *et al.* 2011). As the greater proportion of trap biomass usually leads to increasing the total prey capture, ecological benefit associated with the greater proportion of trap biomass should obviously prevail over the cost associated with the structure and maintenance of the traps, including the support of the commensal community.
7. If capturing animal prey is crucially important for the nutritional benefit of carnivory in *Utricularia*, the strategy of prey capturing could “drive” the evolution of traps in aquatic *Utricularia* species, while the interaction with the trap commensal organisms could be more marginal.

Concluding Remarks: Inspiration For Further Research

It is undeniable that the newest data on the water flow in the traps (trap door buckling, spontaneous firings, and water recirculation) have markedly changed the classic view of trap function. It follows from this review, that it is necessary to reject the commonly accepted view that there is a great nutritional importance on the trap commensal community for the plant in barren waters with low prey availability (*e.g.* Richards 2001). The microbial trap community in traps without animal prey may now be considered as parasites rather than commensals. However, this revised view on the role of trap microorganisms in *Utricularia* traps does not contradict the commonly accepted role of these microorganisms in facilitating prey digestion as commensals but only clearly excludes a nutritional benefit for the plant from their living in traps without prey.

To obtain further insight into the ecophysiology of trap functioning in (aquatic) *Utricularia* species, the following directions of research could be considered and the questions raised could be answered.

1. Electrophysiological studies should resolve the crucial question as to whether *Utricularia* traps are stimulated to fire via the conventional electrophysiological signalling pathway (including a rise in action potential in the sensory hairs) or purely mechanically (*cf.* Sydenham & Findlay 1973; Vincent *et al.* 2011a).
2. As the dominant part of ecophysiological research on *Utricularia* traps has been conducted on aquatic species (they have much larger traps) do the same processes run also in the terrestrial species (*i.e.*, water flows, secretion of enzymes, respiration characteristics, interaction with the commensals, *etc.*)?
3. The discrepancy between very low protease activity found in the trap fluid and high activity found inside secretory vesicles in the quadrifid glands should be elucidated. Moreover, what is the role of commensal microorganisms in prey digestion for different enzyme classes? What is the uptake efficiency of the main mineral nutrients (N, P, K) from prey in the traps?
4. As opposed to the almost zero [O₂] in the trap fluid, the internal trap glands can provide sufficient ATP energy for their demanding functions. Which adaptation allows these glands to provide sufficient ATP energy?

5. The biochemical mechanism of water pumping out of the traps has been insufficiently studied. Can this mechanism be determined using modern experimental approaches (e.g., patch-clamp, vibration probe, ion-sensitive microelectrodes)?
6. Biophysical aspects of trap firing and resetting should be studied in association with the measurement or setting of negative pressure inside the traps as a possible regulatory factor for water pumping. The study should verify the recent concept of continuous water pumping from the traps and water recirculation.
7. Is the pattern of the spontaneous firing associated rather with the mechanical properties of the trap walls or metabolic characteristics of traps?
8. The importance of phytoplankton and detritus as a potential nutrient (N, P, K) source for *Utricularia* in barren waters could be elucidated on the basis of estimation of the matter in the trap fluid and modelling.
9. What is the role of the commensal community in the nutrient interactions within the plant having traps with or without prey? Obviously, the use of sterile plants and their inoculation with commensal microorganisms could be one of the promising approaches.

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NUTRIENT STOICHIOMETRY OF *NEPENTHES* SPECIES FROM A BORNEAN PEAT SWAMP FOREST

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Abstract

To shed light on the nature of nutrient limitation in carnivorous plant communities, we collected data on foliar nutrient concentrations and ratios from three *Nepenthes* species and one natural hybrid growing in peat swamp forests of southern Borneo. Due to their low foliar nitrogen concentrations and very low nitrogen:phosphorus ratios, our data strongly suggest that these species are limited by nitrogen availability.

The carnivorous habit and uptake of nutrients from invertebrate prey items is an evolutionary response to the nutrient-poor environments in which some plants find themselves. To determine patterns of nutrient use and nutrient limitation in carnivorous plants, nutrient concentrations and stoichiometry (ratios between nutrients) can be assessed (Koerselman & Meuleman 1996; Willby *et al.* 2001; Olde Venterink *et al.* 2003; Güsewell 2004). From a review of the literature, Ellison (2006) suggested that most carnivorous plants are phosphorus (P) or nitrogen (N) + P limited but he presented minimal data from *Nepenthes* pitcher plants. Osunkoya *et al.* (2007) went some way towards rectifying this deficit by providing data on N, P, and potassium (K) concentrations from six species in Brunei that suggested that *Nepenthes* are actually N limited due to their very low N concentrations and low N:P ratios. However, this is currently the only study with multi-element data from *Nepenthes* species. In this paper we provide extra much-needed information on *Nepenthes* leaf nutrients from three species and one natural hybrid found in a peat swamp forest in Indonesian Borneo to improve generalizations about nutrient relationships in this fascinating plant genus.

In the Sebangau peat swamp forest in Central Kalimantan, Indonesia (2°18'S; 113°55'E), three species of *Nepenthes*, *N. ampullaria* Jack, *N. gracilis* Korth. (see Fig. 1), and *N. rafflesiana* Jack are found along with one natural hybrid, *N. × hookeriana* Lindl. (Mansur 2008). Leaf material (all leaves were estimated to be less than one year old) was collected from individuals of these four 'species' in April-May 2006. About 40 mg of leaf material was digested in 2.5 ml concentrated sulphuric acid with a lithium sulphate/selenium (100:1) catalyst at 375°C for 4 hours, diluted with deionized water, and analyzed for nutrient concentrations on a Dionex ICS-2000 Ion Chromatography System (for N) or a Varian Vista AX Inductively Coupled Plasma Optical Emission Spectrometer (for all other elements). Differences in nutrient concentrations between species were analyzed by one-way ANOVAs implemented in Minitab 15.1 and data was log₁₀ transformed where needed to improve homogeneity of variances.



Figure 1: *Nepenthes gracilis* growing in peat swamp forest at Sebangau, Central Kalimantan, Indonesia.

Table 1 shows the nutrient concentrations of the four ‘species’. Nitrogen, phosphorus, and calcium all showed generally low concentrations whereas potassium and magnesium were around, or above, average (Grimshaw *et al.* 1989; Pugnaire 2001; Broadley *et al.* 2004). There were no significant differences in N concentrations between the ‘species’. Phosphorus concentrations were greatest in *N. gracilis* and *N. rafflesiana* as were K concentrations (although differences for K were not significant). *N. ampullaria* showed the lowest concentrations for many of the nutrients, including the micronutrients.

Based on prior analysis of species and life-forms from temperate regions, many from wetlands (Koerselman & Meuleman 1996; Willby *et al.* 2001; Olde Venterink *et al.* 2003; Tessier & Raynal 2003), our data suggest N limitation for all the ‘species’ found as they all had very low N concentrations (less than 0.85% in all individuals). In addition, the foliar N:P ratios of 3.3 to 9.3 were exceptionally low (significantly lower values were found in *N. gracilis* and *N. rafflesiana* than *N. ampullaria* and *N. × hookeriana*) where the critical value of N:P is 14, below which N is considered limiting to plant growth (Koerselman & Meuleman 1996) although this value may be lower in drier forests (Tessier & Raynal 2003). P concentrations were also very low in *N. ampullaria* at levels that are considered limiting ($<1 \text{ mg g}^{-1}$; Willby *et al.* 2001) but the low N:P ratio still suggests greater limitation by N in this species. There was no indication of K being a limiting nutrient in any of the ‘species’ examined ($>0.8\%$, N:K $<2:1$, and K:P >3.4 ; Willby *et al.* 2001; Olde Venterink *et al.* 2003).

Our results therefore corroborate the data of Osunkoya *et al.* (2007) who found average nutrient concentration across six species in Brunei to be N = 0.81%, P = 1.9 mg g^{-1} , and K = 1.08% with an N:P ratio of less than 5; Osunkoya *et al.* (2007) also collected leaves from peat swamp forest but these were combined with plants from heath forest for analysis. Their N and P values were higher than ours although their K values were lower and overall they considered that *Nepenthes* species

Table 1. Nutrient concentrations and stoichiometric ratios for nine plant nutrients in four 'species' of <i>Nepenthes</i> pitcher plants in the Sebangau peat swamp forest, Central Kalimantan, Indonesia. Different letters within a row indicate statistically significant differences ($p < 0.05$) using Tukey's tests (on \log_{10} transformed data where required).				
	<i>N. ampullaria</i>	<i>N. gracilis</i>	<i>N. × hookeriana</i>	<i>N. rafflesiana</i>
N (%)	0.50 ± 0.07 (a)	0.65 ± 0.07 (a)	0.67 ± 0.08 (a)	0.63 ± 0.05 (a)
P (mg g ⁻¹)	0.59 ± 0.07 (a)	1.52 ± 0.36 (b)	0.85 ± 0.14 (ab)	1.16 ± 0.09 (b)
K (%)	2.61 ± 0.21 (a)	4.70 ± 0.29 (a)	2.29 ± 0.33 (a)	5.90 ± 1.68 (a)
N:P	8.49 ± 0.41 (b)	4.65 ± 0.59 (a)	8.09 ± 0.39 (b)	5.42 ± 0.32 (a)
N:K	0.19 ± 0.01 (ab)	0.14 ± 0.01 (a)	0.30 ± 0.01 (b)	0.16 ± 0.06 (a)
K:P	45.1 ± 2.3 (a)	34.6 ± 5.3 (a)	27.1 ± 0.6 (a)	49.8 ± 13.9 (a)
Ca (mg g ⁻¹)	0.57 ± 0.09 (a)	1.51 ± 0.86 (a)	6.86 ± 1.13 (b)	1.67 ± 0.31 (a)
Mg (mg g ⁻¹)	2.05 ± 0.38 (a)	5.10 ± 0.36 (b)	6.61 ± 0.58 (b)	9.01 ± 2.47 (b)
Fe (µg g ⁻¹)	7.7 ± 0.8 (a)	40.5 ± 10.6 (b)	60.9 ± 7.9 (b)	73.4 ± 31.0 (b)
Mn (µg g ⁻¹)	9.7 ± 1.6 (a)	57.3 ± 23.9 (b)	251 ± 24 (c)	172 ± 31 (c)
Ni (µg g ⁻¹)	0.41 ± 0.05 (a)	2.13 ± 0.74 (ab)	4.99 ± 1.93 (b)	2.45 ± 0.99 (ab)
Zn (µg g ⁻¹)	5.9 ± 0.6 (a)	21.1 ± 6.2 (a)	66.5 ± 9.3 (b)	17.2 ± 4.1 (a)

were N limited in contrast to other carnivorous plant genera which appear to be P or N + P limited (Ellison 2006).

Most micronutrient concentrations in the *Nepenthes* leaves were normal to low for plant tissues and there were no remarkable concentrations. It was interesting to note that, for *N. × hookeriana*, only in some cases (P, Mg, Fe) were the values intermediate between that of its 'parent' species *N. ampullaria* and *N. rafflesiana*. In terms of other nutrients (Ca and other micronutrients) it had the highest concentrations; perhaps reflecting some aspect of hybrid vigor (Chen 2010).

In conclusion, our results suggest that N is the limiting nutrient for *Nepenthes* in contrast to other carnivorous plants that seem to be P or N limited. This hypothesis may not include montane *Nepenthes* that, somewhat surprisingly, appear to have higher foliar N concentrations (Clarke *et al.* 2009). However, the only way to fully determine the nature of nutrient limitation is through fertilization experiments although this presents difficulties of its own as differences have been found in plant responses to fertilization through the leaves as compared to the roots (Adamec 1997). More work is clearly required on the mineral nutrition and nutrient stoichiometry of Asian pitcher plants.

Acknowledgements: CIMTROP are thanked for research permission and David McKendry and Paul Warren are thanked for assistance with nutrient analyses.

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DROSERA REGIA STEPHENS

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Keywords: Cultivation: *Drosera regia*

Much has been written about this interesting species of sundew over the years, both in the popular literature and indeed on-line in more recent times. Much of what is written would serve to discourage the average hobbyist from attempting cultivation, and as a result until surprisingly recently *Drosera regia* was scarcely seen. The truth however, is that this plant is generally easy to grow successfully, and once established is a long lived perennial which can attain huge dimensions.

Although it is becoming commoner in peoples collections, it remains exceedingly rare in the wild, with one of the smallest and most endangered natural ranges of any *Drosera* species. It is found in a single remote valley at Bainskloof, near Cape Town in South Africa at an altitude of 600-900 m, where it exists as two separate colonies, one of which could possibly already be extinct (pers. comm.) It has been suggested that the two colonies differ by one having slightly broader leaves. Here they are found growing amongst dense grasses which make them somewhat difficult to find, and indeed they compete with the surrounding vegetation by producing their sword-shaped lanceolate leaves up to 50 cm in length—the largest of any *Drosera*. At their bases the leaves can be up to 2 cm wide, gradually tapering to a point at their apex, with many large tentacles up to 4 mm in length, each topped with a generous droplet of mucilage found on the upper surface of the leaf, facing inwards toward the growth point (see Fig. 1). The rear of the leaves is glabrous, with a large raised central vein which runs the entire length. They are a uniform bright apple green color, with the central vein being slightly lighter, and suffusing red at their base by the growth point (see Fig. 2).

Producing leaves of this size enables the plant to capture insect prey of a substantially larger bulk than other species, and unlike other upright species such as *Drosera filiformis* from North America, and *Drosera graminifolia* from South America, *Drosera regia* has not only active tentacles, but is able to curl its leaves along their entire length. This power of movement ensures that the plant can catch and hold prey as large as the common wasp *Vespula vulgaris*, the leaves often folding over more than 360° in the struggle.

The large amount of mucilage produced by the tentacles mean that this species catches many more insects than others, and its leaves can become black with insect carcasses.



Figure 1: Close up of *Drosera regia* leaves.



Figure 2: Red leaf bases of *Drosera regia*.



Figure 3: Adult *Drosera regia* plants.



Figure 4: *Drosera regia* plants emerging from dormancy.

lose their growth, producing a kind of loose hibernacula of tiny truncated leaves sometimes barely 1 cm in length (see Fig. 4). At this time they are fairly tolerant of low temperatures, enduring the occasional freeze. With the increase in day length, growth resumes in early March, and within one month they can produce a rosette of 4 or 5 mature leaves which unfurl watch-spring-like until they are fully open.

The first flush of leaves are followed by flower stalks which are easily recognisable as they are circular in cross section, glabrous, and with a narrowly ovate embryonic bud covered in short,

This plant has the unusual characteristic of producing a rhizome, which is clothed by dead leaf bases and which, periodically, divides into two branches. Over many years the whole plant can become very large with numerous growth points. My original plant, which is now over 18 years old, has 6 such growth points and over-hangs its 35-liter pot. It is approximately 60 cm across with leaves usually in excess of 45 cm in length, produced each year (see Fig. 3).

Their growth pattern is fairly similar to many other South African *Drosera* species. Over winter when the light levels drop, they



Figure 5: Glandular *Drosera regia* calyx lobes.



Figure 6: The stigmas are simple and un-receptive.

stalked red glandular hairs—protection from sap sucking insects (see Fig. 5). The flower scapes are usually taller than the leaves and can branch several times, so a single stem may support as many as 20 flowers. The flowers themselves are spectacular, up to 3 cm in diameter, bright pink with darker pink veins running the length of each petal, with the green glandular calyx lobes holding their bases together so that a tube is formed, from which emerge the anthers and



Figure 7: Receptive, fimbriate stigmas, clearly visible.

stigmas. This species is usually regarded as being self sterile, but the flowers have a mechanism for reducing the risk of self pollination. Bright yellow pollen is released copiously shortly after opening, but at this time the stigmas are simple, unbranched, and un-receptive (see Fig. 6). Once the pollen has been released, the stigma tips open and feather out, becoming fimbriate (see Fig. 7). When this occurs, the flower can be pollinated with pollen from another flower (although some residual pollen may be released from the same flower). Several flowers open together to give a better chance of seed-set, and I have obtained a good quantity of seed from single clones. The seeds are falcate and 2 mm in length (see Fig. 8). Of course, having more than one clone is preferable as the resulting progeny are likely to be more variable and vigorous.

After flowering, growth continues, with each growth point producing several more leaves, which toward the end of the season become progressively shorter as autumn approaches. With the onset of winter, the glandular leaves die back and dormancy begins.

Despite what has written about this plant, it is easy to grow in cultivation and as I've already stated is long-lived. Mine grow in the same bed as my other summer growing South African species such as *D. capensis*, *D. admirabilis*, and *D. slackii*, with a southerly aspect in full sun, and stood in 2-3 inches of rain water for the growing season. Over winter the water is reduced down so as the compost remains damp, but doesn't dry out. I use a silver sand and peat moss mix to a ratio of 60% sand and 40% peat which gives good results.

Seed is the best method of producing a number of plants, but it is somewhat slower than in other species. Seed appears not to require any pre-treatment and can be surface sown on plain peat moss in the spring and early summer. Keep in a sunny position and in a tray of rain water, and germination commences in 3-5 weeks. I find it best to leave the seedlings until they are at least 2 cm in height before potting separately in to 7-8 cm pots in the same compost as mentioned above.

Root cuttings work well, and can easily be taken without disturbing the adult plant (which



Figure 8: Close-up of fresh *Drosera regia* seed.

they seem to dislike, by the way), as they frequently grow out of the drainage holes of their containers and can simply be cut off. Reduce each root to 5 cm in length, and lay on the surface of peat moss. Cover lightly with some torn sphagnum moss, water well from above with rain water, and enclose in a plastic bag to maintain a high humidity. Keep in a bright position away from direct sunlight to avoid overheating, and check weekly. In approximately 4 weeks, the roots will produce tiny green buds which will develop into new plants. Once they are growing well, gradually harden off the plants by making a small hole in the bag, in-

creasing the size of it a little each day for a week, at which time the bag can be removed. As with the seedlings, leave the young plants until they are 2 cm in height before potting separately. The cuttings are best taken in the spring.

Seed grown plants are occasionally available at the nursery website at www.hccarnivorousplants.co.uk

A SURPRISE IN THE GLOAMING:
A FIELD OBSERVATION AT SPLINTER HILL BOG PRESERVE, ALABAMA

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This fall, I had the great pleasure of taking a carnivorous plant tour of Georgia, Florida, and Alabama with Mike Wang. It was a lifetime dream fulfilled, full of amazing plants and treasured memories.

We arrived at Splinter Hill Bog Preserve near Rabun, Alabama late in the day, having been distracted along the way by many smaller roadside sites. We pulled into the parking lot and as we did, our mouths dropped as our hearts rejoiced in unison. There before us were perfectly managed fields of big healthy *Sarracenia leucophylla* at their peak of growth. Spectacular!

The sun was just setting as we leapt from the car to walk through them and hurried to take as many photos as we could while the light held. Soon, it was too dark for photography and I even put my camera away in the car, but I couldn't bring myself to leave yet. It was an amazing moment in my life to be there standing in a sort of carnivore Shangri-La, surrounded by plants that I have loved so much for as long as I can remember (see Back Cover). I never wanted to leave.

We stayed well after sunset and as I walked the paths lined with lacey white pitchers, a creature buzzed past my head. I tried to make out in the darkness what it was, but it was quick and dusky colored, so I strained to find it again. As my eyes raced from pitcher to pitcher in hot pursuit, I quickly noticed two things: that they were everywhere and they were hummingbird or sphinx moths! There were hundreds of them buzzing like little brown fairies from pitcher to pitcher. They beat their wings very rapidly and so they fly less like a moth and more like a hummingbird, hence the name. It is this ability that allows them to hover in front of the pitcher mouth and rob the sweet nectar without paying the ultimate price paid by other visitors. I quickly retrieved my camera and half due to my persistence and half to their abundance I was able to shoot several photos of them (see Fig. 1). They were very charismatic so I chased them in the dark for about an hour, my flash occasionally shattering the dark and mimicking the thunderstorms in the distance. At one point, I was lucky enough to catch one in a moment's rest atop a pitcher lid, which allowed for close inspection and some amazing photos.

They seemed to suffer no ill effect from the nectar as they were all quite aware of my presence. Each one would only partially accept my pursuit for a few pitcher visits before flying far away to another thick patch to eat unbothered. Their very long tongues allow them to avoid the pitcher mouth almost entirely and they are mostly too big to be caught. Casual inspection of the pitcher found no captured moths, so there is no obvious benefit to the plants, but who knows what tiny contribution they might make.

I have since looked up the moth and believe it to be *Enyo lugubris*, the mournful sphinx. This moth is very widespread and ranges all the way from northern Argentina and Uruguay north through Central America, the West Indies, and Mexico to Arizona; east to Florida and north to South Carolina. Adults can be seen in flight year-round in its tropical range including Southern Florida and Louisiana. North of that, adults only fly from August-November. Due to the large numbers all partaking in the same activity and their apparent immunity to the drugging effects of the nectar, I believe that this may represent a significant part of the adults' diet in this area. I wonder even if the flight of adults is timed with the peak pitcher production for *S. leucophylla* in areas where their ranges overlap. It would take much more observation to verify this and unfortunately I live over 2000 miles away, but I would encourage other local enthusiasts to pick up on this initial observation and see if this is a yearly event or just a one night chance sighting.

Bob Hanrahan's ranch is only about 45 minutes from Splinter Hill and he said that he had never seen these moths, but they would be easy to miss in the autumnal evening light.

I love the way these plants have evolved and how over the millennia they have created a micro-cosm of tiny creatures interacting within a complex ecology. It has been my pleasure to share this tiny portion of that world with you.



Figure 1: Hummingbird moths feeding on *Sarracenia leucophylla* at the Splinter Hill Bog Preserve near Rabun, Alabama after sunset.

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DROSERA BURMANNII: A CARNIVOROUS PLANT SPECIES FROM EASTERN GHATS OF INDIA

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The eastern Ghats range of southwestern India, in the coastal part of Andhra Pradesh and Orissa state, is an area rich with diverse plants species. This area has a year-round subtropical climate with a temperature range between 15-25°C and heavy monsoonal rainfall.

While I was describing a new species (*Caralluma moorei* Aditya), I found a very red-colored *Drosera burmannii* Vahl, a well-known insectivorous sundew plant. The plants were growing on the eastern side of Panchlingeswar Hills – an area of open valley grassland. They were found in habitat associated with stony, gravel-rich, and very moist reddish alluvial soil (see Fig. 1).

The Panchlingeswar Hills are a part of the Kuldiha Wildlife Sanctuary in the Balasore [Baleswar in Oriya language] district of Orissa state. Plants from many diverse genera are found here, including *Caralluma moorei*, *Caralluma diffusa*, *Sanseveria* sp., *Bombax malabaricum*, *Gyrocarpus americana*, *Euphorbia nerefolia*, *Ceropegia bulbosa* var. *bulbosa*, many fern species, a few ground orchids, and Liliaceae sp.

At the time, I could not identify the *Drosera* plants, because the species flowers only in January and February, and I was too early. So I visited the area again in January to see if I could find flowering plants. This time I found many plants with bud formation, two near to flowering, and one with a small seed pod. As I waited for a bit of sunshine, the plants showed pinkish flower buds, but did not fully open. I guessed that the plants might be *Drosera burmannii*, a deep red clone found in India. Actually, this species is widely distributed from Australia, Japan, eastern Asia, and also subtropical India. The plants' color depends on sunshine – plants are more greenish under low light.

In cultivation, the plants grow quite well in my cool orchid house (see Fig. 2). I give them a soil mixture of one part sand, one part soil, and one and half part leaf mold with some added old bone meal. The soil is kept moist.



Figure 1: Panchlingeswar Hills, eastern Ghats Ranges.

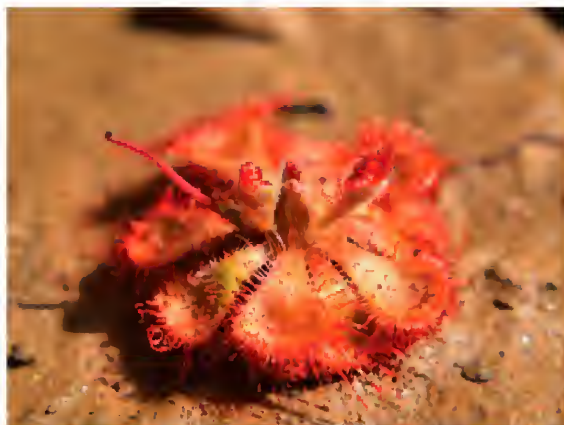


Figure 2: *Drosera burmannii* plants in cultivation.

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NEW CULTIVARS

Keywords: cultivar: *Dionaea muscipula* 'Blanche Hermine', *Sarracenia* 'Jeremy', *Sarracenia* 'Illuminated Hut', *Sarracenia* 'Pomegranate', *Sarracenia* 'Saxapahaw'.

Dionaea muscipula 'Blanche Hermine'

Submitted: 20 January 2012

Dionaea muscipula 'Blanche Hermine' is a white sport from a variegated Venus Flytrap that I found in May 2008 at the Carniflora open day. In September, I was able to take a bulb cutting. The mother plant died from frost during winter 2008/2009.

A small very white plant started to grow from this bulb cutting. I thought that this white plant would die once the reserves of the cutting were exhausted. To see this plant resuming growth in spring 2009 was quite a big surprise for me! The plant must certainly still have had some chlorophyll traces in its leaf, hardly visible in the white leaf tissue (see Fig. 1). *Dionaea muscipula* 'Blanche Hermine' is quite a slow grower because of the deficiency of chlorophyll, but it is possible to do leaf and bulb cuttings to maintain the unique features of this plant.

Blanche Hermine is a very good white beer produce in Britain, where the plant was born. It's also a small animal of the family of Mustélidae (*Mustela ermina*) which one sees everywhere in Europe. In winter, its fur becomes very white except the end of the tail which remains black. When a leaf starts to die the trap becomes black; the contrast with the white remainder of the petiole makes me think of the winter dress of *Mustela ermina*.

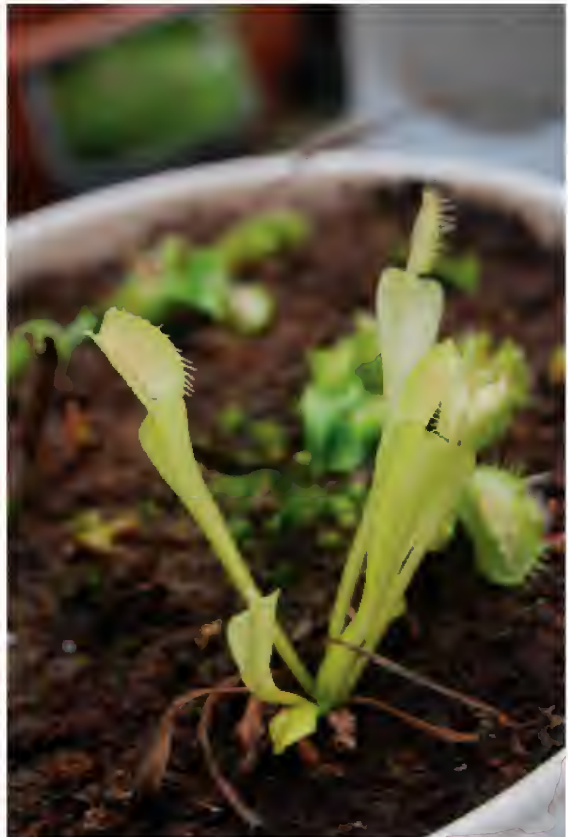


Figure 1: *Dionaea muscipula* 'Blanche Hermine' – a white Venus Flytrap.

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Sarracenia 'Jeremy'

Submitted: 11 April 2012

Sarracenia 'Jeremy' was a cross made by pollination of *Sarracenia leucophylla* and *Sarracenia* \times *mitchelliana* (*S. purpurea* \times *S. leucophylla*) in 1999. I sowed the seed and selected one seedling which after 5 years revealed red flowers like the parents and the pitchers resemble a blend of the colorful venation of *Sarracenia leucophylla* with more upright and narrower pitchers than exhibited by *Sarracenia* \times *mitchelliana*. The epithet refers to my son's name. The pitchers grow to a height of 40 to 45 cm with a lid that is wavy with a rich, red venation under it (see Fig. 2). Right now the rhizome is divided and each one has a flower spike. The plant grows quite vigorously and the best pitchers grow in the fall like the *S. leucophylla* parent which last a long time before going dormant.



Figure 2: *Sarracenia* 'Jeremy' pitcher and flower.

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Sarracenia 'Illuminated Hut'

Submitted: 3 February 2012

I developed *Sarracenia* 'Illuminated Hut' by transferring the pollen from a tall, vigorous *S. leucophylla* onto the stigma of a (*S. purpurea*) × (*S. × courtii*) that has short pitchers and appear pink to light purple in full sunlight. Both parent plants have a dark red petal color. The pollination was made on 22 January 2008. Seeds began sprouting on 11 June. The plant is just over three years old and the adult pitchers have so far attained a height of 38 cm.

Unlike many *S. purpurea* or *S. psittacina* hybrids, this particular plant has characteristics very similar to *S. leucophylla* due to the ruffled lid, fenestrations on the lid, and its tall habit. In contrast to *S. leucophylla*, the lid and top section of the pitcher takes on a bright pink coloration, the pitchers are shorter than the parent *S. leucophylla*, and have a sturdy habit. Furthermore, the lid is slightly opened at the top, allowing for the opportunity of a small amount of rainwater to enter the pitchers (see Fig. 3). This plant has not flowered so far, although it is expected to in a year's time.

A very strong plant, *S.* 'Illuminated Hut' is resistant to short periods of heavy rain, maintaining its upright growth. The attractive color of the lid and mouth region of the pitcher attracts flying insects. The lid's shape takes on the roof of a hut, hence the term "Hut", and the fenestrations on the lid, hence the term "Illuminated". I coined this name in October 2011. This plant needs to be propagated by rhizome divisions to maintain its characteristics.



Figure 3: *Sarracenia* 'Illuminated Hut'. Photo taken January 2011.

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Sarracenia 'Pomegranate'

Submitted: 3 February 2012

I developed *Sarracenia* 'Pomegranate' by transferring the pollen from a (*S. × willisii*) × (*S. × mitchelliana*) to the stigma of a *S. oreophila*. The pollination occurred on 2 October 2006 and the resultant plant is currently in its 4th year of growth. The flower scape had snapped off of the seed capsule plant early in January 2007 and I dried the seed capsule in an open dry plastic container outdoors in a shaded area. On 13 January, inspection of the flower pod revealed two mature seeds that I sowed on pure peat moss on the same day. By July, only one of the seeds had sprouted.

The pollen parent has short, very thin dark red pitchers, whereas the ovary parent is a pure green form of *S. oreophila* that produces tall pitchers 60 cm in height. The pollen parent produces red petals reminiscent of *S. purpurea*, whereas the ovary parent produces yellow petals. The resultant hybrid has flowered for two years in a row, the first time in spring 2010 and a second time in 2011. Petals are a light red color. No seeds have been produced to date. This plant is quite vigorous, producing new divisions relatively fast. Pitchers are tall, reaching up to 40 cm and are generally green with a red tint on the lid and the top section behind the pitcher. The lid has a unique appearance, taking on almost an inverted spoon shape and is pointed (see Fig. 4). The external surface of the pitcher is green in color, whereas the internal surface is heavily veined. I coined the name "pomegranate" on 29 February 2012 as the red coloration on the lid is reminiscent to the surface of a pomegranate fruit. This plant should be propagated by divisions to maintain its characteristics.



Figure 4: *Sarracenia* 'Pomegranate'.

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Sarracenia 'Saxapahaw'

Submitted: 16 May 2012

A specimen of the original plant was sent to me by James Stoner in the winter of 2009. Two years passed and this plant grew to a stunning size in the spring, summer, and fall of 2010 and 2011. The plant exhibits outstanding colors and size and spreads vigorously in our gardens. I quickly contacted James regarding the background of this plant and began researching it myself. Despite James' and my attempts, no background information was found. I believe the plant was mislabeled in the past so very little history on the plant's origin exists.

In the spring the plant sends up reddish pitchers tipped with 2-4 cm of blended bright yellow coloration. When the pitchers open, their insides are filled with pale yellow with distinct streaks of red veining patterns throughout the underside of the hood and their outer surfaces are speckled with pink reticulations (see Fig. 5 left). Once the plant is established for more than one year, tall pitchers up to 70 cm begin to darken throughout the summer season, the pitchers transition to burgundy, and peristomes change from a deep burgundy to ruddy brown in bright sun (see Fig. 5 right). The peristome widths range from 6 to 8 cm wide. Pitchers may reach sizes larger than recorded measurements if grown in bright conditions and left for repeated seasons without dividing. In fall this process repeats itself. The parental background of this plant is a mystery. It appears that this plant has ancestry from *Sarracenia flava* var. *atropurpurea* and *S. leucophylla*. The flowers are dark red, similar to *S. leucophylla* with pale blotches of yellow on each petal.

Sarracenia 'Saxapahaw' is named after a Native American tribe of North Carolina's Haw River, whose history is also a mystery. Saxapahaw is now a small but eclectic town.

This plant should be propagated by vegetative means only.



Figure 5: *Sarracenia* 'Saxapahaw' form and coloration in spring (left, photo by Fred Passkiewicz) and late summer (right, photo by Victor Holland).

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LITERATURE REVIEWS

by JAN SCHLAUER

Rivadavia, F., Miranda, V. F. O. de, Hoogenstrijd, G., Pinheiro, F., Heubl, G., and Fleischmann, A. 2012. Is *Drosera meristocaulis* a pygmy sundew? Evidence of a long-distance dispersal between Western Australia and northern South America. *Annals of Botany* 110(1): 11-21.

Essentially the present paper answers the initial question by a loud and clear “yes”, providing compelling evidence from germination pattern (cryptocotylar), pollen morphology (aperture type 7-8), chromosome number ($2n = 32, 34, 36$ with equal frequency), DNA data (*rbcL* sequence homology nests *D. meristocaulis* within sect. *Bryastrum* – the pygmy sundews, ITS+*rps16* homology place it sister to the same), and leaf trichomes (stout, short yellow gland-like trichomes with four-celled peduncle and a glandular head on petiole present, but the eight-celled biseriate microglands characteristic for sect. *Bryastrum* are missing in *D. meristocaulis*). The only disturbing fact that remains is the occurrence of *D. meristocaulis* in the Neblina massif at the Brazil/Venezuela border, separated from the remaining pygmy sundews by the whole extent of the Pacific Ocean. But even this disjunction is not completely unknown to plant geographers, as admitted by the authors.

The impressive list of similarities mentioned in the paper above can be augmented by a personal observation by the reviewer (JS), as an investigation of dried material of *D. meristocaulis* (kindly provided by Fernando Rivadavia) for naphthoquinones did not reveal any detectable amount of plumbagin nor of 7-methyljuglone. These acetogenic compounds are distributed throughout the genus *Drosera* with the notable exception of sect. *Bryastrum* that apparently lacks them whatsoever.

Heřmanová, Z. Kvaček, J. 2010. Late Cretaceous *Palaeoaldrovanda*, not seeds of a carnivorous plant, but eggs of an insect. *Journal of the National Museum (Prague), Natural History Series*, 179(9): 105-118

The paper discloses with reasonably good evidence that the fossils formerly interpreted as seeds and attributed to a genus *Palaeoaldrovanda* closely related to *Aldrovanda*, are in fact fossilized insect eggs. Several Tertiary *Aldrovanda* fossil seeds, seeds of the recent *A. vesiculosa* and different insect eggs are compared by scanning electron microscopy demonstrating the microstructural similarities among the *Aldrovanda* seeds and significant differences of these to *Palaeoaldrovanda* that position the latter closer to the insect eggs. In particular, according to the authors “*Palaeoaldrovanda* is not a seed with a basic anatropical and bitegmic organisation; there is no evidence of a raphe, and the wall structure is simple. *Palaeoaldrovanda* does not show a clearly pronounced micropyle or chalaza. (...) Our new interpretation of *Palaeoaldrovanda* significantly influences the current view of the family Droseraceae. It is at least possible that this family did not evolve until the Tertiary. It may also influence the hypotheses of the first unequivocal appearance of carnivorous plants in general.”

The following two papers that appeared in Carnivorous Plant Newsletter should be viewed from this new perspective:

Degreef, J.D. 1997. Fossil *Aldrovanda*. *Carniv. Pl. Newslett.* 26(3): 93-97

Schlauer, J. 1997. Fossil *Aldrovanda* - Additions. *Carniv. Pl. Newslett.* 26(3): 98

BOOK REVIEW

by MARCEL VAN DEN BROEK

Bourke, G., and Nunn, R. 2012. Australian Carnivorous Plants. Hardcover, 180 pp., 180 images, ISBN: 978-1-908787-02-6. Redfern Natural History Productions. £29.99/£34.99 (signed/unsigned) + shipping from redfernnaturalhistory.com.

In front of me is the latest publication from Redfern, this time not from the hand of Stewart McPherson but “Made in Australia” by natives.

Greg Bourke and Richard Nunn are two carnivorous plant enthusiasts with a well-deserved reputation in fieldwork and photography. They combined their knowledge and passion to produce a book about the carnivorous plants of their native land.

Let me start by stating what this book isn't: It is not the long awaited and desperately needed field guide to the carnivorous plants of Down Under. But if not that, then what is it and why should you buy it?

It's somewhat ungainly size (31.5 cm wide and 24 cm high) proclaims exactly what it is: A coffee table book and a superb one at that.

Not much for detailed text I'm afraid, but a wealth of high quality photographs from all over this island continent adorn this book.

All families of carnivorous plant are mentioned in this work, as indeed are a very large number of actual species. The writers claim to have given the first complete listing of all currently known species of Australian carnivorous plants. With the continuous discovery of new plants and the reclassification of botanical status based on our advancing knowledge it is highly likely that when you read this book several change will already need to be made, but everyone will have to agree that this is the most complete work on the subject to date and is impressive by any standard.

Each section starts with a short text giving the highlights of the botanical history of the family, some information on the structure of the plant, its trapping mechanism, the distribution, and its habitat.

A nice touch is the short texts labeled “Photographic Challenge”, giving an insight into the problems of photographing the plants.

While I frankly would have liked more information on growing conditions, this is a very good book. The highly detailed pictures of each species are a feast for the eye and the stunning shots of the Australian landscape make you want to run to the airport and fly over.

The book ends with a section on the conservation status of carnivorous plants in Australia naming not only the usual suspects as human influence as a main source, but also the lack of human influence. Many species have evolved not only with but also because of 40,000 years of fire stick farming and now modern Australian society is very much focused on the prevention of fires to protect property and people. Also global changes in the weather is predicted to see the demise of several species, for example, *Drosera arcturi* is only found on the highest and coldest peaks and those places are getting scarce.

All in all this is a great book to dream away with and at £29.99, a very reasonably priced book at that.

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